The Coevolution of Whitebark Pine and Clark's Nutcracker

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Coevolution is said to be occurring when two (sometimes more) species interact in such a way that the evolution of both is affected, due to selective pressures each exerts on the other. This process shapes evolutionary changes in such interactions as predator/prey, seed/seed disperser, and parasite/host situations, in which each participant in the interaction exerts natural selective pressures on the other(s).

A coevolutionary relationship can be direct, as when two species affect each other; or diffuse, when a species' evolution is shaped by numerous other species, which are in turn affected by it. The former is exemplified by the coevolved mutualism between whitebark pine *(Pinus albicaulis)* and Clark's Nutcracker *(Nucifraga columbiana)*; the latter by the mutualism between the tropical tree *Caesaria corymbosa* and its numerous seed dispersers which include woodpeckers, flycatchers and vireos.

A mutualism is an interaction between species in which each contributes essential benefits to the other. As a default position, it can be argued that mutualisms are of necessity coevolved. Another possibility that might account for a mutualistic relationship is the coadaptation of two species. This implies that the species had already evolved traits that allowed a mutualism to come about between them when they fortuitously encountered each other. However, such a chance meeting would probably rapidly become coevolutionary.

The mutualism of whitebark pine and Clark's Nutcracker exemplifies that which involves the other stone pines of *Pinus* subsection *Cembrae* and the Eurasian Nutcracker, *N. caryocatactes.* The nutcracker regenerates the pine by caching its seeds in the soil as a stored food and failing to eat all of them, or feed them to its young. Those that germinate form the only reliable nucleus of a new generation. In honing the relationship between these species the pine has been caused to deviate from its progenitor white pines in the morphology of its seeds (large and flightless), cones (non-opening, breakaway scales that clasp seeds, sessile attachment), branching (verticalized cone-bearing branches, limb forking to amplify cone production and form a display surface), and in the variable dormancy of its seeds (postponing germination and allowing the nutcracker's food source to remain available).

The other members of subsection *Cembrae* are the Swiss stone pine (*P. cembra),* Siberian stone pine *(P. sibirica),* Korean stone pine *(P. koraiensis),* and Japanese stone pine *(P. pumila).* Except perhaps for *P. pumila,* which some investigators believe is misplaced in this subsection, the other stone pines share with whitebark pine, to a surprising degree, the morphological modifications described above. In addition, no other species in this large and

variable genus share the cone modifications that characterize the stone pines. This is true even of other bird- or mammal-dispersed pines like limber pine *(P. flexilis)* and the pinyons *(*subsection *Cembroides)* that share some seed and form characters.

The nutcracker has deviated from its *Corvidae* progenitors by evolving an exceptional memory, a powerful bill, a unique sublingual pouch for seed transport, and a suite of behavioral traits that optimize its seed foraging activities. The dependency of the pine on the nutcracker for its regeneration, and of wildlife species not a part of the mutualism for pine seeds, demonstrate the indispensability of biodiversity in maintaining ecosystem integrity. This mutualism also spotlights how a lineage of passerine birds has engendered phylogenetic diversity in an ancient lineage of conifers.

Can the coevolution of whitebark pine and Clark's Nutcracker be demonstrated as actually having occurred, or is it a presumption? Playing Devil's Advocate, I would argue that all relationships viewed as coevolutionary are indeed presumptions which by their nature cannot be demonstrated. That is because the genetic changes required of each interacting species, probably the fixation of mutant genes, cannot be directly observed. And even if they could, each such change could only be presumed to be caused by selective pressure from the opposite participant, and not from some other organism or factor acting in parallel. What basis, then, have we for labeling the pine-corvid relationship coevolutionary?

The answer, I believe, lies in the empirical evidence of modification from white pine progenitors on the one hand, and corvid progenitors on the other. Each of the white pine modifications figures in the foraging by nutcrackers for pine seeds. It appears highly improbable that such a suite of characters could arise one by one over the millions of years of this interaction without a natural selective impetus. The same holds true for the nutcracker characters that depart from those of other corvids. Things fit together too nicely and work too efficiently for us to ascribe them to coincidence with any confidence.

A few words should be said about the ecological effects of the mutualism of corvids and stone pines. Whitebark pine is a pioneering species, usually seeded by nutcrackers in burned areas or other openings. Many are sown by nutcrackers in the shade of the forest as well, but those that begin their lives in the open are more likely to survive to maturity. As a result, the whitebarks that come up in the open are in a position to materially modify their environment, from a treeless area to one supporting a woodland of scattered, broad crowned, low-branched trees or tree clumps with large cone-bearing capacity.

The modified microclimate they create by providing shade, reducing wind speed and raising relative humidity permits the establishment of wildflowers, shrubs and forbs absent from the openings on their margins. Birds and mammals that find the openings inhospitable, move into the woodland groves. Eventually, shade tolerant conifers – firs and spruces – form an understory and eventually replace the whitebark pine canopy. On very exposed sites whitebarks may provide the only tree cover for centuries. Whatever the ultimate outcome, whitebark pine is a species of uncommon value, and its disperser, Clark's Nutcracker, is complicit in all that the pine brings about. Thus it is the landscape and its biodiversity that are the legacy of this instance of coevolution.